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Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado

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Abstract

Aim There is increasing research attention being given to the role of interactions among natural disturbances in ecosystem processes. We studied the interactions between fire and spruce beetle (*Dendroctonus rufipennis* Kirkby) disturbances in a Colorado subalpine forest. The central questions of this research were: (1) How does fire history influence stand susceptibility to beetle outbreak? And conversely, (2) How does prior occurrence of a beetle outbreak influence stand susceptibility to subsequent fire?

Methods We reconstructed the spatial disturbance history in a *c.* 4600 ha area by first identifying distinct patches in the landscape on aerial photographs. Then, in the field we determined the disturbance history of each patch by dating stand origin, fire scars, dates of mortality of dead trees, and releases on remnant trees. A geographical information system (GIS) was used to overlay disturbance by fire and spruce beetle.

Results and main conclusions The majority of stands in the study area arose following large, infrequent, severe fires occurring in *c.* 1700, 1796 and 1880. The study area was also affected by a severe spruce beetle outbreak in the 1940s and a subsequent low-severity fire. Stands that originated following stand-replacing fire in the late nineteenth century were less affected by the beetle outbreak than older stands. Following the beetle outbreak, stands less affected by the outbreak were more affected by low-severity fire than stands more severely affected by the outbreak. The reduced susceptibility to low-severity fire possibly resulted from increased moisture on the forest floor following beetle outbreak. The landscape mosaic of this subalpine forest was strongly influenced by the interactions between fire and insect disturbances.

Keywords

dendrochronology, *Dendroctonus*, disturbance, interactions, legacies, fire, subalpine forest, Colorado.

INTRODUCTION

There is increasing research attention being given to the role of interactions among natural disturbances in ecosystem processes (e.g. Paine *et al.*, 1998; Turner *et al.*, 1998; Frelich & Reich, 1999). Many disturbances do not act in isolation and synergism has long been recognized as a component of disturbance regimes (White & Pickett, 1985). Nevertheless, while much research has focused on various parameters of natural disturbances such as distribution, frequency, size, and magnitude, relatively little research attention has been given to the synergism or interactions among disturbances.

Most disturbance regimes are affected not only by climatic (e.g. Johnson *et al.*, 1990; Veblen *et al.*, 2000) and topographical factors (e.g. Swanson *et al.*, 1988; Foster & Boose, 1992; Kramer *et al.*, 2001), but may also be affected by the site's disturbance history (e.g. Veblen *et al.*, 1994; Kulakowski & Veblen, 2002). Large infrequent disturbances can leave long-lasting legacies which affect subsequent ecological processes. Fire and insect disturbances have been shown to interact and synergistically affect forest succession, nutrient cycling, species composition, and diversity (McCullough *et al.*, 1998). For example, interactions between stand-replacing fires and outbreaks of spruce beetle (*Dendroctonus*

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rufipennis Kirkby) have been suggested to exist in Colorado subalpine forests. Colorado subalpine forests are dominated by *Picea engelmannii* (Parry) Engelm. (Engelmann spruce), *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), *Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine), and *Populus tremuloides* Michx. (quaking aspen) and are shaped primarily by large, infrequent, and severe fires, which generally occur during extremely dry years (Rebertus *et al.*, 1992; Peet, 2000; Veblen, 2000). Low-severity fires also occur under certain conditions but play only a minor role in shaping stand structure and the landscape mosaic (Sherriff *et al.*, 2001; Sibold, 2001). Outbreaks of spruce beetle can be very severe, causing mortality of most canopy size Engelmann spruce over areas of hundreds of square kilometers (Hinds *et al.*, 1965; Schmid & Frye, 1977). As spruce beetles primarily attack large trees (Schmid & Hinds, 1974), susceptibility of young stands to outbreak is lower (Veblen *et al.*, 1994; Bebi *et al.*, 2003). Conversely, mortality caused by spruce beetle may increase susceptibility to fire by increasing the abundance and continuity of fine and coarse fuels (Hopkins, 1909; Knight, 1987). However, there was no increase in fire density (frequency per area) in beetle-affected stands during the 50 years following a severe outbreak in White River National Forest (Bebi *et al.*, 2003). This suggests that an increase in fire hazard may exist for only several years following the outbreak before dead fine fuels decay. Alternatively, an increase in fire risk because of the increase in dead fuels may have to be coincident with appropriate climatic conditions following the outbreak in order to be realized. Analysis of fire–beetle interactions based on interpretation of aerial photographs over a large area (e.g. over 700 km^2; Bebi *et al.*, 2003) can lend valuable insight into broad spatial associations between these disturbances. Finer-scale dendroecological analysis of individual stands (i.e. patches $<$ *c.* 250 ha) can complement such studies by describing disturbance interactions with greater spatial and temporal accuracy and by considering low-severity disturbances which may not be detectable through remote sensing.

We hypothesized that legacies of fire and spruce beetle disturbances will affect the subsequent disturbance regime. We used dendrochronological techniques and a geographical information system (GIS) to study the interactions between fire and spruce beetle disturbances in a Colorado subalpine forest. The central questions of this research were: (1) How does a stand's fire history influence that stand's susceptibility to beetle outbreak? And (2) How does the occurrence of a beetle outbreak in a stand influence that stand's susceptibility to subsequent fire?

STUDY AREA

The study area is located in an area of northwestern Colorado that was affected by a severe spruce beetle (*D. rufipennis*) outbreak in the 1940s, which reached its peak in 1947 (USDA Forest Service *unpublished survey data*). We chose the present area because, in addition to having been affected by the beetle outbreak, it represented a variety of stand structure and cover type based on a preliminary USDA Forest Service cover type map (USDA Forest Service, 1993) and a historical map of late nineteenth century fire occurrence (Sudworth, 1900). This area lies within the Flat Tops Wilderness in White River National Forest (107°15′ W, 40°00′ N). The *c.* 4600-ha area is approximately bound on the east by Himes Peak, on the south by the Flat Tops plateau, on the west by Sable Point, and on the north by grasslands adjacent to the North Fork of the White River. The study area ranges in elevation from 2450 to 3250 m (8000–10,650 feet) a.s.l. (Fig. 1). Forests are dominated by *P. engelmannii* (Engelmann spruce), *A. lasiocarpa* (subalpine fir), *P. contorta* (lodgepole pine), and *P. tremuloides* (quaking aspen). Based on our field observations, this area has no history of extensive logging.

The closest climate station to the study area is Marvine Ranch which is located at 2380 m (7800 feet) a.s.l. and which has a climate record from 1972–98 (Colorado Climate Center, 2001). The mean January temperature is −8.5 °C and the mean July temperature is 14.2 °C. Mean annual precipitation is 668 mm.

METHODS

Field methods

The *c.* 4600 ha study area was stratified by identifying internally-homogeneous patches of forest on 1 : 40,000 colour infrared aerial photographs (minimum mapping unit = 5 ha). At this scale, not more than 10% of points on the photograph are in error by more than 20.3 m (USGS, 1947). Based on this stratification, 54 internally-homogeneous patches were delineated within the study area and a sampling point was subjectively located in a representative area within each patch. This method of mapping based on identifying distinct patches on aerial photographs has been widely used as a starting point to reconstruct disturbance histories (Heinselman, 1973; Johnson & Gutsell, 1994; Veblen *et al.*, 1994; Kipfmueller & Baker, 2000; Kulakowski & Veblen, 2002).

Field data were collected from May–August 2000. Stand disturbance history was reconstructed using dendrochronological methods. Subalpine forests in the Southern Rocky Mountains are characterized mainly by large, infrequent, stand-replacing fires (Romme & Knight, 1981; Romme, 1982; Rebertus *et al.*, 1992; Turner & Romme, 1994; Kipfmueller & Baker, 2000; Kulakowski & Veblen, 2002). In such a case, stand age is a good approximation of the time since the last stand-replacing fire (Johnson & Gutsell, 1994; Kipfmueller & Baker, 1998). Within each patch, a sampling point was subjectively located in a representative area. In order to obtain stand-origin dates, increment cores were collected from ten to fifty-six of the largest live and dead trees within a *c.* 300 m search area around the sampling point. The number of trees cored depended on the difficulty of preliminarily assessing the disturbance history of each patch based on examination of tree cores in the field. Stand structure (i.e. canopy dominance, presence and/or dominance of subcanopy and understorey) was qualitatively

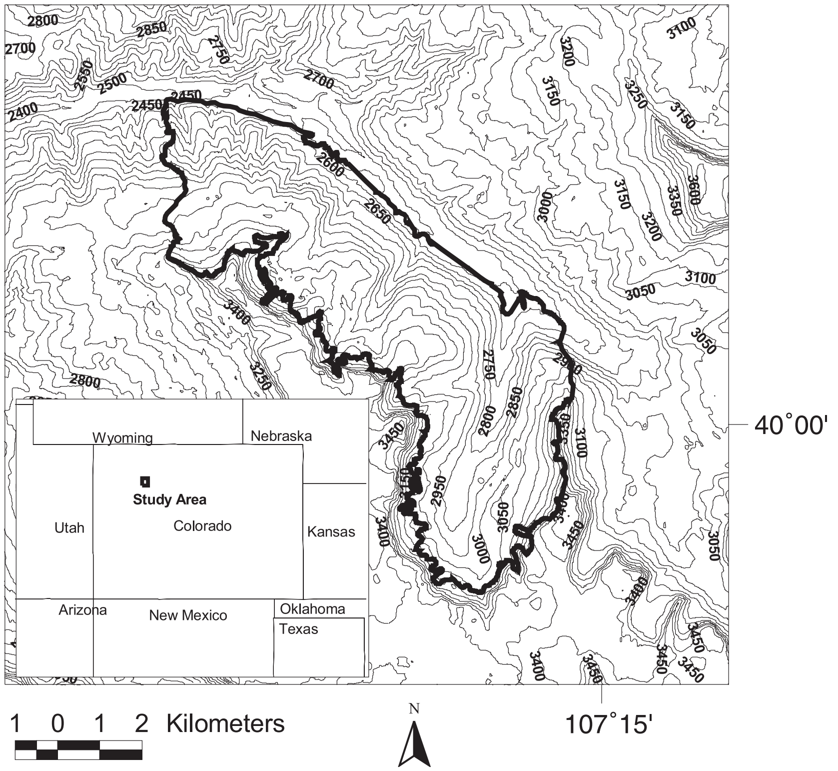

Figure 1 Location and topography of the study area (50-m contour interval).

described in each patch. If size structure of a stand was comprised of >1 unique cohort (e.g. a bimodal size structure), then cores were collected from trees of each cohort. Testing in similar forests has shown that subjectively selecting the largest trees gives a better estimate of time since fire than randomly selecting trees (Kipfmueller & Baker, 1998). These trees were cored as close to the ground and to the pith as was possible. Increment cores from a total of 825 trees were successfully processed. Based on ages of tree seedlings from similar nearby forests (Veblen *et al.*, 1991c; Kulakowski & Veblen, 2002), error associated with the difference between actual tree age and age at coring height is relatively small and therefore is unlikely to be a source of error in our interpretations of fire history. Therefore, tree age is reported as age at coring height. In order to determine the exact year of occurrence of stand-replacing fires or other low-severity fires, the study area was systematically searched for fire-scarred trees and samples were collected as they were encountered, within patches and along patch boundaries. Fire-scarred trees were rare, but forty-seven partial cross-sections of fire-scarred trees were collected (McBride & Laven, 1976). The location of fire-scarred trees was recorded using the global positioning system (GPS).

In order to assess the severity of the 1940s outbreak, in each patch five 10×10 m plots were located at 30-m intervals along a zigzagging transect. The direction of the transect was random and changed at 30-m intervals (at each plot location). Within each plot d.b.h. of all canopy trees (i.e. ≥20 cm d.b.h.) was measured and species and status as living or dead was recorded for each tree.

Sample processing

Standard procedures were used to process fire-scar wedges (McBride, 1983) and increment core samples (Stokes & Smiley, 1968). In the event that the increment core sample missed the pith, a simple geometric model was used to estimate the number of rings to the pith (Duncan, 1989). This method was used to estimate a maximum of twenty missing years to the pith. Cores that missed the pith by > 20 years were counted as minimum ages. To date the establishment and mortality of dead trees and to address the problem of missing and false rings, cores and wedges were cross-dated visually using marker years (Stokes & Smiley, 1968) or were measured and cross-dated using the program COFECHA (Holmes, 1983).

Reconstruction of stand disturbance history

Disturbance reconstruction was focused on large disturbances by fire and beetle. In older forests, fine-scale gap-phase dynamics certainly affect stand development, and such fine-scale processes were not considered by the present research protocol. The aim of this study was to examine disturbance interactions at a stand scale rather than at the scale of the individual tree or small (e.g. 10 m^2) patch.

Stand disturbance history was reconstructed based on stand-origin dates, fire-scar dates, dates of mortality of dead trees, releases (abrupt >200% increases in ring width sustained >10 years) in remnant trees, and Forest Service documents (e.g. unpublished survey data). No evidence of other extensive disturbances (e.g. blowdown) was found in the study area, and, thus, the sampling effort was aimed at describing the history of fire and spruce beetle outbreaks. A small portion of forest near tree line was chronically disturbed by avalanches. Methods of reconstructing fire history are as those described in Kulakowski & Veblen (2002). Because fires that shape Colorado subalpine forests are primarily large, severe, and infrequent, our primary aim was to group stands into broad age classes that most likely arose following such fires. To do so, dates of establishment of the oldest trees in each stand were used as an approximation of the year of the last stand-replacing fire. Allowing for a lag time between the fire and seedling establishment, the stand-origin date may indicate the approximate time of such a disturbance. When possible, the stand-origin date was refined by temporally proximate occurrence of fire as indicated by precisely dated fire scars. Old-growth stands typically have a broad range of ages among the largest trees in comparison with post-fire stands. The potentially long period of gap-phase dynamics in old-growth stands eventually exerts a more dominant effect on stand structure than the initial stand-replacing fire. In contrast, post-fire stands typically have identifiable pulses of establishment. The occurrence of lower severity fires was reconstructed based on dating and mapping of fire scars and, in some cases, an associated second cohort within an otherwise older stand.

Methods of reconstructing history of spruce beetle outbreak are as those described in Veblen *et al.* (1991a). Outbreaks of spruce beetle result in coincident mortality of large (>10 cm d.b.h.) Engelmann spruce and lodgepole pine during the outbreak and coincident releases (abrupt and sustained increases in growth pattern) of the surviving trees (Veblen *et al.*, 1991b). The occurrence of the 1940s beetle outbreak was determined in each sampled stand by checking tree cores for coincident releases in living trees and dating the year of mortality of dead trees. The severity of the outbreak in each stand was estimated in each stand as the per cent of ≥20 cm Engelmann spruce and lodgepole pine that were dead within the 100 m^2 plots.

Analysis of the interaction between disturbances

Patch boundaries were entered into the Arc 8 (ESRI, 2000) GIS for analysis. Each of these polygons was then assigned attributes of the date of the last stand-replacing fire, the occurrence of any lower severity fires, and severity of beetle outbreak. Overlay analysis (ESRI, 2000) was used to describe the relationship between fires and beetle outbreak. Overlay analysis tabulates the total area of all values of one variable, which occur in each value of a second variable. This observed amount is then compared with the expected amount, which is proportional to the amount of total area in that category. If a given variable does not influence a stand's susceptibility to beetle outbreak, then the amount of area affected by the outbreak in each class of that variable is expected to be proportional to the amount of area affected by the outbreak in the whole study area. Thus, a positive departure of the observed from the expected indicates greater susceptibility to beetle outbreak and a negative departure indicates lower susceptibility.

Because a census was conducted of all patches >5 ha in the study area, it was not necessary to use inferential statistics to evaluate statistical significance of differences in attributes among classes of patches. However, to avoid attributing ecological significance to possible measurement error, our interpretation only emphasizes patterns where differences among observed and predicted patterns are large (>10%).

RESULTS

Reconstruction of stand disturbance history

Fire-scar dating showed fire occurrence in the study area (using a criteria of a minimum of two trees scarred) in 1796, 1856, 1864, 1875, 1880, 1911, 1927, 1930, 1935, 1950 and 1961 (Fig. 2). However, we found no evidence of post-fire establishment for the majority of these fire dates. We interpreted the fifty-four patches to be the result of four different stand-origin classes (Fig. 3; Table 1). The *c.* 4600 ha study area is composed of old-growth forest, two old post-fire cohorts, and a young post-fire cohort. Old-growth forest makes up 168 ha (4%) of the study area (Fig. 4; Table 2), and in this study is defined as having no evidence of fire in at least >300 years. Stands in this category had heterogeneous age structure among the largest canopy trees. The oldest trees in each old-growth stand dated from AD 1570 to 1680 (Fig. 3; Table 1).

The oldest post-fire cohort occupies 2483 ha (58%) of the study area and was interpreted to originate in *c.* 1700 (Fig. 4; Table 2). Stands in this category exhibited establishment of canopy trees beginning from 1700 to 1780 (Fig. 5; Table 1). There were no fire scars associated with this cohort. Thus, the interpretation of the fire date was based on establishment dates of rapidly growing trees, the oldest of which dates to 1700.

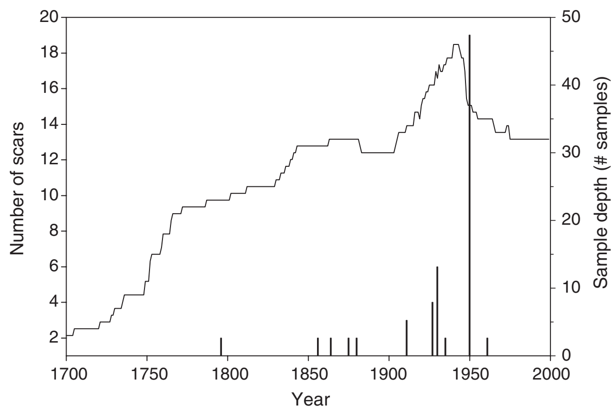

Figure 2 Number of partial cross-section samples recording scars (bars). Eleven years showed the occurrence of fire in the study area using a criteria of a minimum of two trees scarred. Horizontal line indicates sample depth.

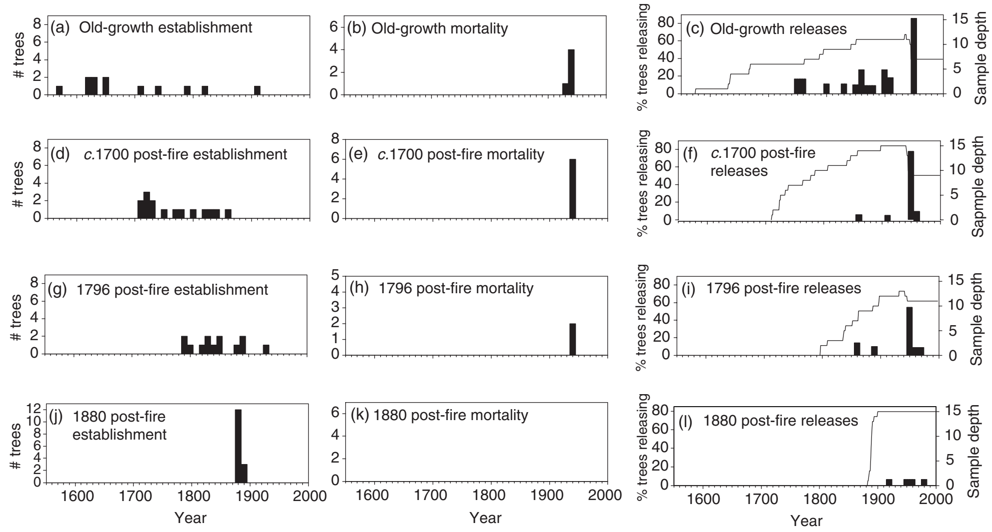

Figure 3 Dates of establishment, mortality (last complete year of growth), and releases in 10-year classes in a typical old-growth stand (a–c), in a *c.* 1700 post-fire stand (d–f), in a 1796 post-fire stand (g–i), and in a 1880 post-fire stand (j–l). Horizontal line indicates sample depth (no. of trees).

The second oldest post-fire cohort occupies 938 ha (22%) of the study area and was interpreted to originate after a fire in 1796 (Fig. 4; Table 2). Stands in this category exhibited establishment of rapidly growing canopy trees beginning from 1796 to 1840 (Fig. 3; Table 1). Two fire-scarred trees show the occurrence of fire in 1796.

Forest stands covering 675 ha (16%) were initiated after a fire in 1880 (Fig. 4; Table 2). This interpretation is based on coincident establishment of rapidly growing trees beginning from 1882 to 1906 among stands in this cohort (Fig. 3; Table 1). Two fire scars show fire occurrence in 1880. Several stands in this category had at least one remnant tree that survived the otherwise stand-replacing fire (Table 1). While this fire was stand-replacing in most of the study area, it also affected 205 ha (5%) with moderate severity. This interpretation is based on the presence of a *c.* 1880 cohort in otherwise older stands.

The majority of the study area (3534 ha; 83%) was affected by the historically-documented 1940s spruce beetle outbreak with severity of ≥20% mortality of canopy size (≥20 d.b.h.) *Picea* and *Pinus* (Fig. 5). Stands that were interpreted to have been affected by beetle outbreak were characterized by trees which showed coincident mortality from 1946 to 1949 (mode 1947) and coincident releases of surviving trees (Fig. 3). No evidence of earlier outbreak was found.

In 1950, 450 ha (11%) of the study area was affected by a low-severity fire (Fig. 6). Samples from nineteen fire-scarred trees recorded fire in 1950 in *Picea-Abies* and *Pinus* dominated stands (Fig. 2). The structure of affected stands was primarily single-tiered and homogenous. Increment core samples did not show coincident releases, which would have suggested mortality of canopy trees and consequential release of resources and reduction in competition. Cross-dating of dead trees did not reveal mortality of trees associated with this fire. Similarly, ages of trees do not indicate presence of a second cohort. Thus, following this fire, no evidence of significant new tree establishment was found. While a few smaller trees may have been killed and a few others may have been released, no significant effect on stand structure was detected. No scars or other evidence of this fire were found in adjacent *Populus* dominated stands.

Effect of fire history on pattern of beetle outbreak

Because the study area was dominated by stand-replacing fires rather than less severe fires prior to the beetle outbreak (Figs 4 and 7), the analysis focuses on the former (i.e. on the 1880, 1796 and *c.* 1700 post-fire stands and on old-growth stands). The three oldest stand-origin classes were affected by beetle outbreak more than expected if fire had no effect on beetle susceptibility, and the youngest (1880) post-fire class was affected less than expected (Fig. 8). However, there was no difference in susceptibility to beetle outbreak among the three oldest classes. Because of possibly confounding influence of cover type, a separate analysis was conducted excluding aspen-dominated stands and considering only those dominated by conifers. When only these conifer-dominated stands were considered, the relative susceptibility of post-fire classes does not change (Fig. 9).

Effect of beetle outbreak on pattern of fire

Because the 1950 fire occurred at lower elevations (below 2985 m), overlay analysis was conducted of the beetle outbreak and the 1950 fire for the part of study area below 2985 m a.s.l. This fire was contained primarily in stands that were not affected by beetle outbreak. Stands with no or low (0–19%) beetle caused mortality were affected more than would be expected while stands in the same elevational zone

Table 1 Dates of establishment of the oldest trees in each stand, the presence (Y) or absence of remnant trees, the total number of trees increment cored in that stand, the stand-origin class to which that stand was assigned, and the canopy dominance

Stand no.	Date of establishment of oldest tree	Remnant trees	Number of trees	Stand-origin class	Canopy dominance
2145.21	1906*		13	1880	*Pinus*
1819.02	1900†		17	1880	*Pinus*
1819.03	1899†		16	1880	*Pinus*
1890.00	1899*		16	1880	*Populus*
2034.00	1896†		15	1880	*Picea–Abies*
2161.00	1895†	Y	15	1880	*Picea–Abies*
2143.00	1894†		18	1880	*Picea–Abies*
1986.00	1894*		13	1880	*Picea–Abies*
2105.00	1891*	Y	13	1880	*Pinus*
1865.00	1890†		13	1880	*Pinus*
1896.00	1887†	Y	15	1880	*Picea–Abies*
1903.00	1883*		16	1880	*Pinus*
2039.00	1882†		12	1880	*Populus*
2985.00	1840†		19	1796	*Picea–Abies*
2145.24	1836†		15	1796	*Picea–Abies*
2145.18	1832†		12	1796	*Picea–Abies*
2277.00	1823†		10	1796	*Populus*
2145.20	1811*	Y	12	1796	*Picea–Abies*
2242.00	1807†		11	1796	*Populus*
2145.01	1802*	Y	19	1796	*Picea–Abies*
2145.19	1801‡		15	1796	*Picea–Abies*
2145.03	1800†		15	1796	*Picea–Abies*
2145.08	1796†	Y	13	1796	*Picea–Abies*
2145.14	1790†		16	1700	*Picea–Abies*
2164.00	1776†		10	1700	*Populus*
2145.02	1775†		15	1700	*Picea–Abies*
2132.00	1773†		11	1700	*Picea–Abies*
2001.02	1771†		11	1700	*Picea–Abies*
2719.00	1768†		14	1700	*Picea–Abies*
2145.26	1767†		15	1700	*Picea–Abies*
2145.25	1758†		20	1700	*Picea–Abies*
2145.10	1756†		11	1700	*Picea–Abies*
2145.15	1755†		12	1700	*Picea–Abies*
2145.11	1739†	Y	15	1700	*Picea–Abies*
2145.13	1734†		14	1700	*Picea–Abies*
2001.03	1733‡		10	1700	*Picea–Abies*
2145.05	1730†		13	1700	*Picea–Abies*
1921.00	1728*		16	1700	*Picea–Abies*
2100.00	1725†		15	1700	*Picea–Abies*
2350.00	1724†		14	1700	*Picea–Abies*
2145.23	1724*		15	1700	*Picea–Abies*
2145.27	1722†		19	1700	*Picea–Abies*
2145.28	1720*		56	1700	*Picea–Abies*
2069.00	1716*		18	1700	*Picea–Abies*
2145.04	1712†		28	1700	*Picea–Abies*
2001.01	1712*		10	1700	*Picea–Abies*
2145.12	1707†		15	1700	*Picea–Abies*
2145.22	1705†		15	1700	*Picea–Abies*
2145.06	1702†		13	1700	*Picea–Abies*
2145.17	1700*		20	1700	*Picea–Abies*
1819.01	1680†		11	Old-growth	*Picea–Abies*
2145.16	1676†		13	Old-growth	*Picea–Abies*
2145.07	1672†		14	Old-growth	*Picea–Abies*
2145.09	1570†		13	Old-growth	*Picea–Abies*

*Pith date.
†Approximate pith date based on Duncan's (1989) method.
‡Innermost year.

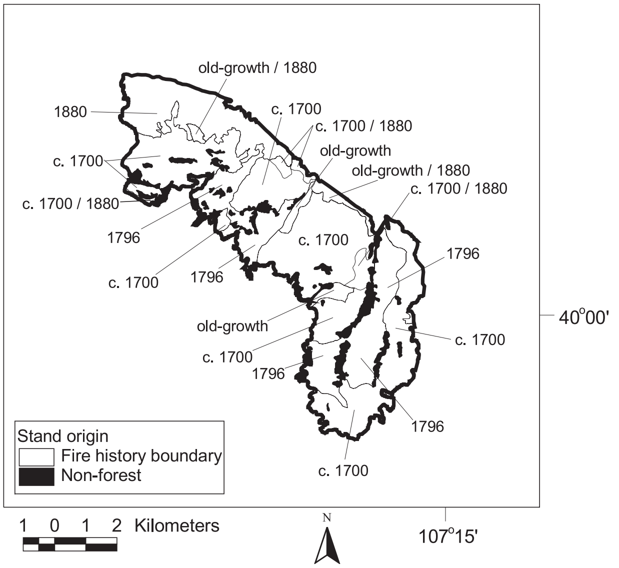

Figure 4 Fire history classes in the study area. Dates correspond to the year of the last stand-replacing fire. For classes with two dates, the first date is the date of stand-replacing fire and the second is the date of moderate severity fire.

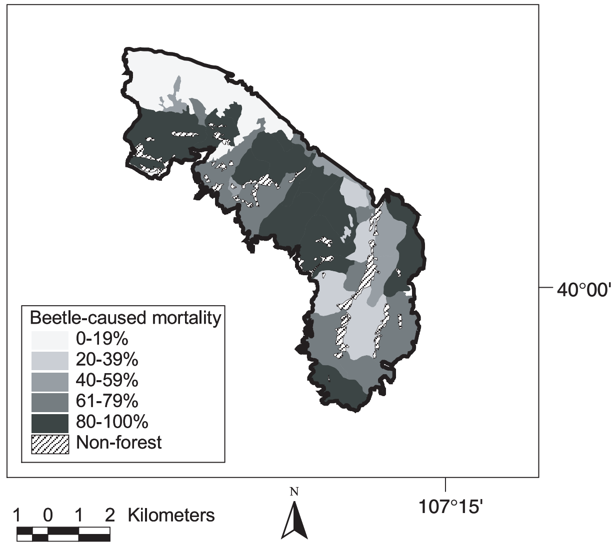

Figure 5 Severity of the 1940s *Dendroctonus rufipennis* Kirkby (spruce beetle) outbreak in the study area. Severity is expressed as percent mortality among canopy (>20 cm d.b.h.) *Picea* and *Pinus*.

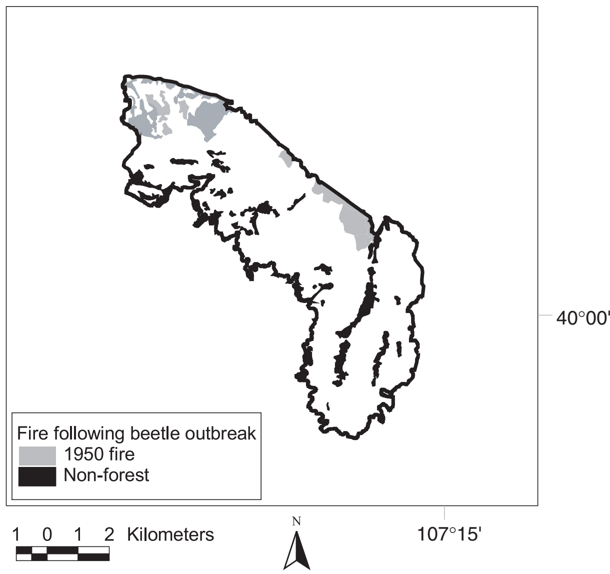

Figure 6 The 1950s low-severity fire in the study area.

Table 2 Classes of stand origin based on dendrochronological interpretation of stand-origin dates, radial growth patterns, and fire-scar dates

Class	Range of dates of oldest trees in each polygon	Number of trees increment cored	Number of corresponding fire scars	Total area ha	%
1880 post-fire	1882–1906	192	2	675	16
1796 post-fire	1796–1840	141	2	938	22
c. 1700 post-fire	1700–1790	441	0	2483	58
Old-growth	1570–1680	51	n/a	168	4

with moderate to high (20–100%) beetle caused mortality were affected less than expected (Fig. 10).

DISCUSSION

Reconstruction of stand disturbance history

The majority of the study area (96%) established following three severe fires (Fig. 7). This interpretation is based on stand-origin dates for relatively large patches of homogenous forest structure. While post-fire cohorts often exhibit a relatively narrow range of establishment dates among the oldest trees, the establishment dates in the present study cover a broader range. There are several contributing reasons for this phenomena. First, there is often a lag between stand-replacing fire and tree re-establishment. The length of this lag can be affected by the size of the burn, the availability of seed, climate, and other factors (Peet, 1981; Alexander, 1984; Rebertus *et al.*, 1992). Secondly, there is an inherent difficulty of locating the oldest trees in stands as those stands get older (Kipfmueller & Baker, 1998). Thirdly, the broad range is also due to the sampling of both dead and live trees in stands that were affected by beetle outbreak. The large dead trees, which were killed by spruce beetle, were often the oldest trees in each stand. In contrast, the largest live trees that were sampled grew abruptly as a result of being released following the outbreak. Such trees were often much (sometimes >100 years) younger than the

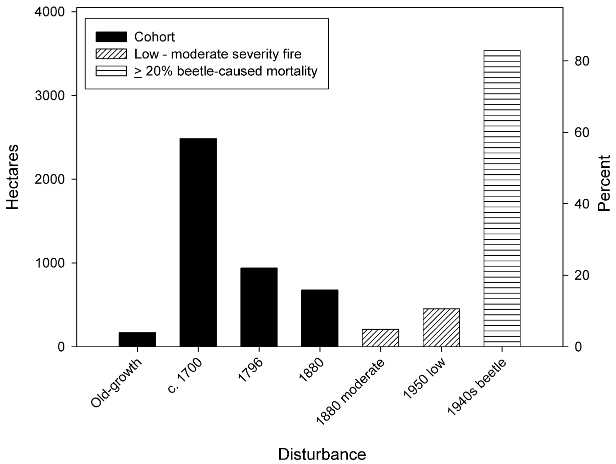

Figure 7 Total area (hectares and percent of the study area) of old-growth stands, old post-fire stands (*c*. 1700 and 1796), recent post-fire stands (1880), moderate severity fire (1880 moderate), low severity fire (1950 low), and forest affected by beetle outbreak in 1940s with >20% mortality of canopy Picea and Pinus.

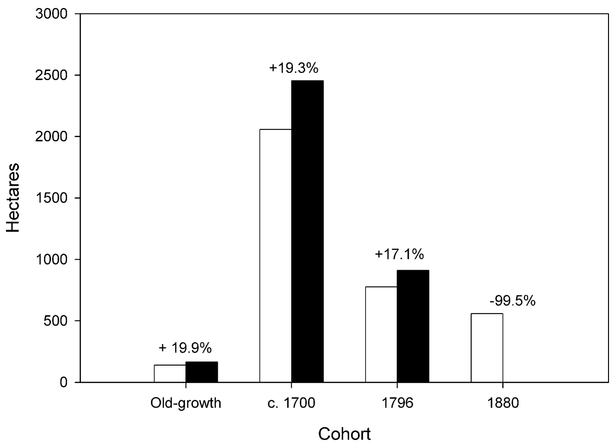

Figure 8 Expected (assuming no effect of time since last stand-replacing fire; open bars) and observed (filled bars) beetle-caused mortality (> 20% mortality) in areas of different fire history for all cover types. Percentages above bars indicate departure from the expected.

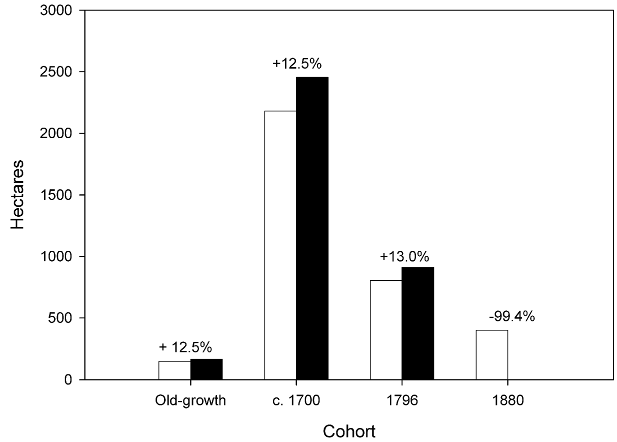

Figure 9 Expected (open bars) and observed (filled bars) beetle-caused mortality in areas of different fire history in conifer-dominated stands (i.e. excluding aspen dominated stands). Percentages above bars indicate departure from the expected.

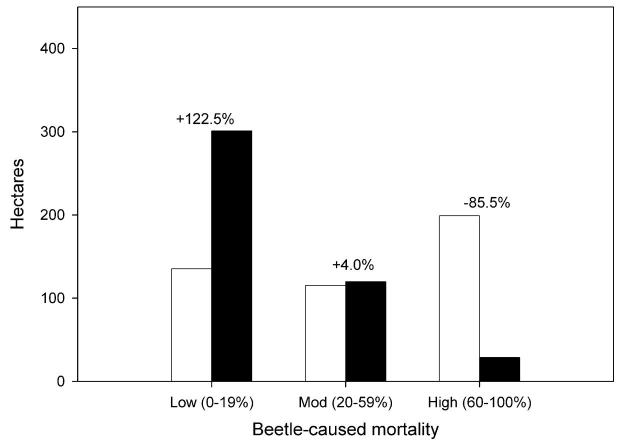

Figure 10 Expected (open bars) and observed (filled bars) low-severity fire (1950) in areas of different beetle-caused mortality (*c*. 1947).

dead trees within the same stand. When this study was initiated, we did not anticipate such a discrepancy between the establishment dates of live and dead canopy trees in post-fire stands. The apparent age-dependent mortality associated with spruce beetle outbreaks is important to consider in studies that reconstruct fire history using stand-origin dates in beetle-affected stands.

One of the major fires in the study area, the 1880 fire, was mostly an extensive stand-replacing fire that left few survivors, but this fire also spread with moderate severity to adjacent forest giving rise to a second cohort within these stands. In these moderate severity areas, the 1880 fire appears to have opened the stand enough to have allowed new tree establishment. In 1950 a wide-spread low-severity fire affected 11% of the study area. This fire likely spread from the grass meadows to the north of the study area and burned up slope through the study area. The 1950 fire was severe enough to scar trees within the area, but it did not cause detectable mortality of established trees and therefore was apparently not followed by an establishment of a new cohort.

Numerous studies have found that subalpine forest structures in the southern Rockies are primarily shaped by infrequent stand-replacing fires (Romme & Knight, 1981; Romme, 1982; Rebertus *et al*., 1992; Turner & Romme, 1994; Kipfmueller & Baker, 2000), although fires may be patchy and of mixed severity in some areas (Bartlett Howe, 2001; Sibold, 2001). While fires in Colorado subalpine forests are typically stand-replacing (Rebertus *et al.*, 1992), the present study area shows evidence of a fire which affected parts of the landscape with moderate severity (1880). In areas of moderately severe burning in 1880, the fire scarred trees and in some cases gave rise to a second cohort. The study area also shows evidence of a low-severity fire (1950), which scarred many trees but did not result in a second cohort. A low-severity fire in 1930 also affected a limited extent of the study area. Previous studies have shown that small surface fires can burn relatively frequently in some habitats near alpine treeline in Colorado (Sherriff *et al.*, 2001) and infrequently in some lodgepole pine and spruce-fir forests (Kipfmueller & Baker, 2000; Sibold, 2001). Thus, although stand-replacing fires are most important in shaping forest structure, surface fires also occur at certain sites. Further research is necessary to document the conditions which are conducive to the occurrence of surface fires within the subalpine zone.

The 1950 fire was recorded by many more fire-scarred trees than any of the large stand-replacing fires which strongly shaped the present landscape mosaic (Fig. 2). While methods of describing a fire regime based on fire scars alone may be appropriate for systems which are characterized mainly by low-severity fires (e.g. ponderosa pine woodlands; Swetnam & Baisan, 1996), these methods are less applicable in systems which are primarily shaped by stand-replacing fires (e.g. subalpine forests in the Southern Rocky Mountains). As the present study illustrates, inference of a fire regime in the latter forest type from the fire-scar record alone would be erroneous. Stand-origin and fire-scar data have been previously combined to study fire regimes in other forest types (e.g. Taylor, 1993; Taylor & Skinner, 1998). We suggest that it is necessary to use a combination of stand-origin and fire-scar dating to reconstruct the actual fire regime of forests that are characterized by stand-replacing fires.

Effect of fire history on pattern of beetle outbreak

Stands that initiated after the 1880 fire were much less affected by beetle outbreak than older stands (Figs 8 and 9). This is consistent with other studies that have found young post-fire stands to be less susceptible to outbreak than older stands (e.g. Veblen *et al.*, 1994; Bebi *et al.*, 2003). During outbreaks, spruce beetles preferentially attack larger trees, especially those >50 cm d.b.h. (Schmid & Frye, 1976). The time between the 1880 fire and the 1940s beetle outbreak was not adequate for trees in most young post-fire stands to reach a large enough size to make them susceptible to beetle attack. Thus, following stand-replacing fire, stands were not susceptible to beetle outbreak for at least *c.* 67 years following the fire. In stands where aspen dominate the canopy, Engelmann spruce may establish at a latter stage of development or there may be so few spruce in the canopy as to reduce the overall susceptibility of the stand to outbreak. However, the youngest cohort of conifer-dominated stands was also overwhelmingly unaffected by the outbreak (Fig. 9).

We emphasize the contrast in susceptibility between stands that established before and after the 1880 fire rather than differences among the older stands for several reasons. The disturbance history of the stands that initiated after the 1880 fire is unambiguous, whereas the disturbance history of the older stands is less so. Furthermore, after several hundred years of development, stands are characterized by highly variable and overlapping ranges of the stand structural attributes that affect susceptibility to outbreak. However, we do note that old post-fire stands (1796 and *c.* 1700) and old-growth stands appear to have been equally susceptible to the beetle outbreak. Thus, we hypothesize that susceptibility to beetle outbreak may not increase linearly with stand development, but rather that there is a threshold, or relatively narrow span of years, in forest development during which susceptibility to *Dendroctonus* greatly increases.

While the occurrence of moderate-severity fire is rare in this forest type, such fires may provide unique research opportunities to study the mechanism by which time-since-fire affects stand susceptibility to beetle outbreak. We suggest that within these stands it is likely that the older cohort suffers high mortality during the outbreak while the younger cohort is not affected by the outbreak. Fine-scale research within such stands is necessary to determine whether individual tree size and age affects susceptibility to beetle-caused mortality or whether broader stand-level characteristics have an overriding effect (e.g. Powers *et al.*, 1999). The former would suggest that fine-scale fire behaviour (e.g. the spatial arrangement of remnant trees at the scale of 100 m^2) determines interactions between fire and beetle disturbances, while the latter would suggest that broader-scale fire behaviour (e.g. the presence or absence of severe fire in the landscape at the scale of >1000 m^2) is more important in these interactions.

Outbreaks of other insects have also been shown to be influenced by fire. Numerous studies have shown that individual trees wounded by low to moderate severity fire may be more susceptible to insect attack (McCullough *et al.*, 1998). In contrast, our research suggests that high severity fires can reduce susceptibility to spruce beetle attack at the landscape scale. In certain coniferous forests, the cessation of formerly frequent surface fires has changed stand structure and composition. In some cases, these changes have increased susceptibility to outbreak of mountain pine beetle and the defoliator western spruce budworm (McCullough *et al.*, 1998). Similarly, in the present study, the occurrence of stand-replacing fires reduced susceptibility to spruce beetle outbreak.

Beetle outbreaks are natural processes in these forests (Veblen *et al.*, 1991b; Eisenhart & Veblen, 2000) and the interactions between fire and spruce beetles have likely been important in shaping the landscape long before Euro-American settlement. Nevertheless, management activities often attempt to prevent or suppress outbreaks. To that end, our research suggests that allowing a natural regime of stand-replacing fires to continue will decrease landscape-scale susceptibility to beetle outbreak. Furthermore, because stand-replacing fires create a mosaic of different age patches, their occurrence may prevent an entire landscape from being affected by a single outbreak. Conversely, a homogenization of the landscape due to suppression of stand-replacing fires may increase landscape susceptibility to outbreak.

Effect of beetle outbreak on pattern of fire

As no severe fire occurred within the study area following the beetle outbreak and prior to field data collection in 2000, the effect of beetle outbreak on the potential for the occurrence of severe fire could not be studied. However, the lack of severe fire during the *c.* 54 years following the outbreak suggests that the occurrence of severe fire following outbreak is not inevitable. Furthermore, a regional analysis of fire occurrence in White River National Forest did not find a higher frequency of fire in beetle-affected stands (Bebi *et al.*, 2003).

On a finer spatial scale, the present study shows evidence of a fire that was widespread within the study area, but which was mostly contained in stands not affected by beetle outbreak. This 1950 fire which followed the beetle outbreak affected much more of the stands that were not heavily affected by beetle outbreak (Fig. 10). Its spatial distribution reflects that of the 1880 fire, which reduced susceptibility to the outbreak. Because the 1950 fire was primarily contained in younger forests, which were also the forests not affected by outbreak, it is difficult to determine whether the spatial distribution of this fire was controlled primarily by stand age or by absence of beetle outbreak. Nevertheless, the behaviour of the 1950 fire does not support the suggested increase of fire hazard in stands affected by beetle outbreak (Hopkins, 1909; McCullough *et al.*, 1998). Beetle outbreaks may have a counter-intuitive effect on the potential of low-severity fire to spread. Stands affected by beetle outbreak may experience increased moisture as suggested by the proliferation of mesic understorey herbs (Reid, 1989), and this increase in moisture may actually decrease the potential of low-severity fire to spread in beetle-affected stands. The fact that 1950 was not an exceptionally dry year in this area likely contributed to the low severity of this fire and its consequent inability to spread into beetle-affected stands. An important research question remains of whether the legacies of beetle outbreaks affect fire spread or severity during extreme drought. It presently appears that in forest types where the fire regime is more dependent on extremely dry weather events than moderate fuel differences, beetle outbreak may, in most cases, have no detectable influence on the potential for stand-replacing fire to occur. To the contrary, outbreak may actually reduce the potential for low-severity fire by leading to increased moisture on the forest floor. The lack of increased fire spread or occurrence in beetle-affected stands suggests that a response of fire-hazard mitigation following outbreak may not be necessary in order to maintain a normal fire hazard.

While the lack of an increase in fire occurrence following severe insect outbreak appears counterintuitive, similar phenomena has been observed in other forest types. For example, the potential of summer fires was low following spruce budworm outbreak in Ontario, Canada (Stocks, 1987). Following the opening up of the canopy, mesic understorey vegetation proliferated quickly. The low fire potential was most likely the result of this increase in herbaceous understorey vegetation following the outbreak.

Interactions between natural disturbances

Interactions between natural disturbances have previously been shown to be important in shaping Colorado subalpine forests. For example, susceptibility to severe wind blowdown is lower among young (*c.* 120-year old) post-fire stands than it is among older stands (Kulakowski & Veblen, 2002). In earlier research on the interactions between fire and spruce beetle outbreaks in northwestern Colorado, relatively young post-fire stands were shown to be less susceptible to spruce beetle outbreak (Veblen *et al.*, 1994). The present study also shows that post-fire stands are reduced in their susceptibility to beetle outbreak for at least *c.* 70 years following stand initiation. Such interactions may be a predictable component of the disturbance regime of these forests. However, a broader-scale analysis of fire–beetle interactions suggests that, while such interactions may be widespread, they may also vary spatially in relationship to topographical variables (Bebi *et al.*, 2003).

Natural disturbances leave legacies on the landscape that affect forest processes long after the initial disturbance. Fires and outbreaks of insect that have a selective preference for particular stand structure or tree species are widespread in temperate and boreal forests (Knight, 1987; McCullough *et al.*, 1998). Interactions between these disturbances are likely to be widespread and to have a significant effect on the vegetation mosaic. In order to more completely understand the ecology and development of forests that are shaped by multiple disturbance types, it is important to consider the effects of such disturbance interactions.

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